



FIGURE 1. Wagner tree of characters in North American Lycopodiaceae. Abbreviations of taxa are as follows: Hup = *Huperzia*; Phg = *Phlegmariurus*; Lyc = *Lycopodium*; Dip = *Diphasiastrum*; Psd = *Pseudolycopodiella*; Lie = *Lycopodiella*; Pal = *Palhinhaea*.

early genera: *Asteroxylon*, *Drepanophycus*, and *Baragwanathia*, all from Lower to Middle Devonian strata. The ligulate, heterosporous lycop-sids, Lepidodendrales, Selaginellales, Pleuromeiales, and Isoetales, apparently constitute separately derived assemblages of evolutionary lines that became established by the Carboniferous. The Devonian elements, commonly known as Protolepidodendrales, eligulate and homosporous, are more logical outside groups for comparison with the modern Lycopodiales and include the three genera listed. The original evolutionary progression probably began in the Upper Silurian: Rhyniopsids apparently gave rise to zosterophylloids, and these to lycopodiophytes, and the first two groups became extinct. The most primitive were the Protolepidodendrales, and they too became extinct, as did the ligulate orders Lepidodendrales and Pleuromeiales. These changes are discussed in numerous textbooks of paleobotany (e.g., Bierhorst, 1971; Taylor, 1981, Thomas & Spicer, 1987). Although there are disagreements on the details of the history of lycop-sids, there is a fair consensus regarding the broad outlines. In addition to outside comparison, we examined trends within and between the subgroups of the present-day Lycopodiaceae. The highly complex and specialized propagative branches of the gemma firmosses, *Huperzia* sens. str., are uniquely derived and found only in this genus; comparisons within (and outside) the family support the conclusion that such bizarre shoots involving a number of character changes represent distinct and mul-

tiple advancements (cf. Stevenson, 1976, and references therein). So it is with such character states as cortical roots, plectosteles, ring meristems in gametophytes, napiform gametophyte thalli, nodular sporangial wall cells, unequal sporangial valves, and many of the other states summarized below. However, a number of obvious specializations found in North American Lycopodiaceae are useless at the generic level since they involve only individual species. These "peripheral" or "autapomorphic" states are obviously advanced within their phylads, but they cannot be used for delimitation of whole genera. They include such advancements as leaf margins toothed, leaf tips hair-tipped, stomates only on abaxial leaf surfaces, blade surfaces glaucescent with epicuticular wax, or rhizome subterranean.

At the generic level there are some striking alternative states for which we can assign no polarity at present. We have no basis for judgment either within or outside of the family. These include the patterns of the root base stele, sculpture of spores, extent of the triradiate groove on the proximal spore face, and the sculpture of the proximal face. A particular problem involves the chromosome base number: The chromosome numbers seem to concentrate around $x = 22, 33, 55, 66,$ and $77,$ with various aneuploidal additions and subtractions (F. Wagner, 1992). Intuitively it might seem reasonable to say that lower ploidal levels are more primitive than higher ones and that fewer aneuploidal changes are more primitive than more, but we cannot be sure that this is so in any particular case. We have been forced, therefore, to use base numbers as they are, as a classificatory tool but without applying phylogenetic directionality. These unpolarized trends are summarized at the end of Table 1 and are represented by letters and numbers there and in the character tree, Figure 1.

POLARIZED CHARACTER TRENDS

The character polarizations we have deduced (numbered in Table 2 and Fig. 1, and in parentheses below) come primarily from comparisons with the members of the outside groups given above, supported by data presented by various authors (e.g., Bruce, 1975, 1976b; Holub, 1975, 1983, 1985; Øllgaard, 1975, 1979, 1987; Wilce, 1965, 1972), as well as by ourselves. The basis for determining directionality is outside comparison (Wagner, 1962, 1969, 1980). The terrestrial habitat is considered primitive. Two trends have occurred away from it: to semiaquatic, i.e., inundated for part of the growing season, (1) and to epiphytic

(2). The former is characteristic of *Lycopodiella* and *Pseudolycopodiella*, the latter the dominant condition of *Phlegmariurus*, some species of which have no doubt experienced reversal. Simple, dichotomous aerial branching is considered ancestral by outside comparison, and there are two different transformations: amplification to extremely complex dendroid habit of the aerial shoots (e.g., *Palhinhaea*) (3), and reduction to simple, unbranched aerial shoots (e.g., *Lycopodiella*) (4). The erect habit of terminal aerial branches is considered basic, and the pendent derived (5). The presence of a well-defined creeping rhizome is presumably the initial state, while the loss of a distinct rhizome is considered derived (6), as illustrated by *Huperzia* and *Phlegmariurus*. The emergence of roots close to their position of origin in the stem stele is the most probable ancestral condition, and the extensive basal migration of roots from the shoot apex downward through the cortex to the level of the substratum before emergence is specialized (7), as in the *Huperzia* group. The branching of the roots themselves was initially most likely isodichotomous and gave way to anisodichotomous (8), as is represented in *Palhinhaea*. In all Lycopodiaceae, evergreen condition of the vegetative aerial shoots is evidently the original one; deciduous components like the upright shoots of *Lycopodiella* are thus advanced (9). The lack of hairs and other emergences is the generalized primary condition, and their presence on stems and/or leaves is specialized and secondary (10). From the most likely original stele, the actinostele, there have been two major directions of change: to a meshed actinostele (like that of *Lycopodiella* and its nearest allies) (12), and to the peculiar and unique condition known as plectostele (like that of *Lycopodium* and *Diphasiastrum*) (11).

Highly evolved lateral branches that afford vegetative propagation are observed only in the genus *Huperzia*. They are complex and involve several, apparently de novo elements—the gemmiphore, the abscission layer, gemma axis, and dorsiventral, distinctively oriented, and modified leaves. The generalized condition for Lycopodiaceae and their outside sister groups is to lack such structures entirely, so that their presence alone is apomorphic (13). The gemma apparatus in *Huperzia* evolved *sui generis* a series of other advancements, namely from radial to bilateral (14) as well as others not used here. Aerial stem branching, judging from the fossil outgroups, was almost unarguably dichotomous in the ancestors, and became unequal (anisodichotomous) in the descendants (15). The ranks of leaves on the aerial shoots have undergone re-

duction in number from 6–12 to only 3–5 (16). The vegetative leaves of the aerial parts were originally monomorphic (e.g., *Lycopodium clavatum*), but became transformed in connection with major changes in overall shoot structure so as to be heteromorphic, as in most species of *Diphasiastrum* (17), in which the branches are cordlike and flattened like *Thuja*. (This trend refers only to adult shoots; the juvenile shoots have isophylly, as illustrated by *Diphasiastrum sitchense*, which is apparently neotenic, maintaining its juvenile condition into maturity.)

Presumably, mucilage canals are derived structures absent in the progenitors. The *Huperzia-Phlegmariurus* assemblage still lacks them, but the type of mucilage duct that is basal in the fertile leaf is present in all other genera (20). Veinal mucilage canals occur only in the vegetative leaves of *Lycopodiella* and *Pseudolycopodiella* (18). However, they are absent from the sporophylls in *Pseudolycopodiella*, being present there only in *Lycopodiella* (19). These different patterns, discovered by Bruce (1975), are treated here as separate trends rather than steps in a single trend, because it is not obvious how or even if the different conditions are sequenced.

Sporophylls in the primitive lycopsids were structurally mostly like trophophylls, as they are today in typical *Selaginella selaginoides* and all species of *Isoetes*, and in the Protolpidodendrales. This condition is retained to a large extent in the firmosses, *Huperzia* and many *Phlegmariurus* species. Nevertheless, differentiated sporophylls are found in all five genera of clubmosses (21). Those of *Lycopodiella* and *Palhinhaea* are only partially transformed. The independent development of distinct sporophylls on tassel-like strobiloids that differ from typical strobili in orientation and appendage structure in *Phlegmariurus* is considered a parallelism or convergence. The attachment of the sporangia is basal in Huperzioideae as in the Devonian outgroups, but becomes pseudopeltate to peltate in all of the other groups (22), and associated with this there is a change from unstalked to stalked (23), but this is found only in Lycopodioideae. Where a true strobilus has been formed, the erect orientation is surely the ancestral one, judging from the outside evidence: the peculiar nodding strobili as found in *Palhinhaea* are derived (24). Where strobili are pedunculate, the leafy condition of the stalk as seen in *Lycopodiella* and *Palhinhaea* is exchanged for the scaly to nearly naked condition seen in *Lycopodium* (certain species), *Diphasiastrum*, and *Pseudolycopodiella* (25). The sporangial valves are primitively equal

TABLE 1. Characters and character states used in this analysis.

Character	Primitive	Advanced	Hup	Phg	Lyc	Dip	Psd	Lie	Pal
1. Habitat	terrestrial	semiquatic	0	*	0	0	1	1	0
2. Habitat	terrestrial	epiphytic	0	1	0	0	*	*	*
3. Branching	simple-dichotomous	complex-dendritic	0	0	0-1	0-1	*	*	1
4. Branching	simple-dichotomous	reduced-unbranched	0	0	0	0	1	1	0
5. Habit	erect	pendent	0	1	0	0	0	0	0
6. Rhizome creeping	present	absent	1	1	0	0	0	0	0
7. Root emergence	immediate	corticular	1	1	0	0	0	0	0
8. Root branching	isodichotomous	anisodichotomous	0	0	1	1	0	0	1
9. Aerial shoot	evergreen	deciduous	0	0	0	0	0	1	1
10. Indument	absent (glabrous)	absent to hairy	0	0	0	0	0	1	1
11. Stele	actinostele	plectostele	0	0	1	1	*	*	*
12. Stele	actinostele	meshed haplostele	0	0	*	*	1	1	1
13. Gemma occurrence	absent	present	1	0	0	0	0	0	0
14. Gemma shape	radial	bilateral	1	0	0	0	0	0	0
15. Branching	dichotomous	anisodichotomous	1	0	0	0	0	0	0
16. Ranks of leaves	6-12	3-5	0	0	0	1	1	0	0
17. Nature of leaves	monomorphic	heteromorphic	0	0	0	1	1	0	0
18. Veinal mucilage canal in trophophyll	absent	present	0	0	0	0	0	1	1
19. Veinal mucilage canal in sporophyll	absent	present	0	0	0	0	0	1	0
20. Basal mucilage canal in sporophyll	absent	present	0	0	1	1	1	1	1
21. Sporophyll	like trophophyll	reduced	0	0	1	1	1	0.5	1
22. Sporophyll attachment	basal	pseudopeltate-peltate	0	0	1	1	1	1	1
23. Strobilus attachment	unstalked	stalked	*	*	0-1	0-1	1	0	0
24. Strobilus orientation	erect	pendent	*	*	0	0	0	0	1
25. Peduncle appendages	leaflike	scalelike	*	*	1	1	1	0	0
26. Sporangial valves	equal	unequal	0	0	0	0	0	1	1
27. Sporangial valves	thick	thin	0	0	1	1	1	1	1
28. Sporangial shape	reniform	globose	0	0	0	0	0	1	1
29. Sporangial nature	non-enclosed	enclosed in cavity	0	0	0	0	0	0	1
30. Sporangium cell wall shape	sinuate	straight-walled	0	0	0	0	1	1	1
31. Sporangium cell wall shape	sinuate	sinuate w/invagination	0	0	1	0	*	*	*
32. Side wall thickenings	evenly thickened	nodular-semiannulate	0	0	*	*	1	1	1
33. Side wall thickenings	evenly thickened	not thickened	0	0	1	1	*	*	*
34. Spore sides	convex to straight	concave	1	0	0	0	0	0	0
35. Spore angles	rounded-pointed	truncate	1	0	0	0	0	0	0

TABLE 1. Continued.

Character	Primitive	Advanced	Hup	Phg	Lyc	Dip	Psd	Lie	Pal
36. Allohomoploid meiosis	normal	irregular	1	0	1	0	0	0	*
37. Nothospeciation	common	rare or absent	0	1	0	0	0	0	*
38. Gametophyte nutrition	holomycotrophic	hemimycotrophic	0	0	0	0	1	1	1
39. Gametophyte position	subterranean	surficial	0	0	0	0	1	1	1
40. Gametophyte meristem	central apex	subterminal, ring	0	0	1	1	0	0	0
41. Gametophyte symmetry	dorsiventral	radial	0	0	1	1	1	1	1
42. Gametophyte shape	buttonlike	rapiform	*	*	0	1	*	*	*
43. Gametophyte branching	unbranched	branched	0	1	0	0	0	0	0
44. Apical outgrowth	absent	photosynthetic lobes	0	0	0	0	1	1	1
45. Apical outgrowth	absent	paraphyses	1	1	0	0	0	0	0
46. Gametophyte pigment	white, gray-brown	orange-brown	0	0	0	1	*	*	*
47. Young sporophyte form	erect	horizontal	0	0	0	0	1	1	1
48. First leaves	microphylls	protophylls	0	0	0	0	1	1	1
49. Foot	large	small	0	0	0	0	1	1	1
50. Protocorm	absent	present	0	0	0	0	0	1	1
Undirected characters									
A. Root base stele	A1. c-shaped; A2. plectostele		1	1	2	2	1	1	2
B. Spore sculpture	B1. foveolate-fossulate		1	1	3	3	2	2	2
	B2. rugulate; B3. reticulate								
C. Proximal face	C1. sculptured; C2. not sculptured		1	2	[+2]	1	2	2	2
D. Triradiate groove	D1. reaching margin		1	1	1	1	1	1	2
	D2. not reaching margin								
E. Margo	E1. absent; E2. present		1	1	1	1	2	2	2
F. Equatorial ridge	F1. absent; F2. present		1	1	1	1	2	2	1

Abbreviations of taxa are as follows: Hup = *Huperzia*; Phg = *Phlegmariurus*; Lyc = *Lycopodium*; Dip = *Diphasiastrum*; Psd = *Pseudolycopodiella*; Lie = *Lycopodiella*; Pal = *Palhinhaea*. * = Not applicable or unknown; scored as 0.

in size, but two of the genera have developed decidedly unequal valves (26). The valves of lycopsid ancestors were probably moderately thick as seen in Devonian fossils and modern Huperzioideae, but became thin in Lycopodioideae and Lycopodielloideae (27). The reniform sporangial type appeared in Lycopsida as early as the Devonian (even in the more primitive Zosterophyllopsida) and is still maintained in most modern lycopsids; however, the advanced globose type is found in two genera, *Lycopodiella* and *Palhinhaea* (28). The sporangia are free on the surface in most taxa, but in *Palhinhaea* they are enclosed in specialized cavities (29). In two of the major groups of lycopsids, the sporangial cell walls are characteristically sinuate, but in the third they have become straight-walled (30). The sinuate-walled condition has evolved a different complication, namely, distinctive invaginations, as in typical *Lycopodium* described by Øllgaard (1975) (31). The side walls of the sporangia are typically evenly thickened, but in the Lycopodielloideae, they have specialized nodular or semiannulate thickenings, which are undoubtedly advanced (32). Typical *Lycopodium* species have side wall cells that are not thickened at all, another apparent derivation (33).

The spores of Lycopodiaceae possess many characters, some of which (see above) cannot be polarized with our present knowledge. There are, however, likely initial states for certain features. For example, the equatorial sides of lycopsid spores were most likely convex to straight, as attested by the spores of most lycopsid fossils and even *Selaginella* and *Isoetes*. In one group of extant Lycopodiaceae, *Huperzia* sens. str., the equatorial walls are concave, certainly a specialization (34). Likewise, the spore condition of truncate rather than pointed corners is a derived condition (35). Both of these conditions separate the genus *Huperzia* from *Phlegmariurus*.

Hybridization between species would be expected on theoretical grounds to produce offspring still capable of undergoing normal meiosis. Only as the species accumulate specific incompatible genetic factors does the meiotic behavior become irregular, with progressive loss of pairing ability (36). This derived condition within members of a genus, the usual state in most pteridophytes, is notable in the genus *Huperzia*. However, three other genera, *Lycopodium* sens. str., *Diphasiastrum*, and *Lycopodiella*, are conspicuous because their members can still form apparently fertile hybrids with normal meiosis and spores, i.e., the theoretical primitive state. These genera have not yet lost pairing ability. Very little is known of hybridization

in the remaining groups. There is a profound difference between the capability and results of hybridization within the groups that we do know, so we have used this as a character. If we are correct, the trend of the units within genera should be from interspecific nothospeciation with allohomoploid fertile hybrids, to interspecific nothospeciation with allopolyploid sterile hybrids, to very rare hybrids, to genera with no hybrids at all between their species. Thus, being able to form many hybrids between its component species (of any degree of fertility) is a more primitive condition within a genus than being able to form hybrids only rarely or never (37).

Some of the most prominent differentiations between present-day Lycopodiaceae pertain to the gametophyte generation. It has long been known that some groups have wholly subterranean gametophytes that are mycoparasitic, while others are surficial and have photosynthesis (38). The claims of Freeberg & Wetmore (1957) that these are environmentally determined conditions are no longer accepted, as stated above. We now regard photosynthetic gametophytes in Lycopodiaceae as probably specialized for the following reasons: (a) the species that show them are mainly aquatic, or semiaquatic; (b) the aquatic habitat is not suitable for the growth of subterranean gametophytes; and (c) the basal part of the photosynthetic gametophyte is fleshy and not similar to the ferns and most liverworts. The photosynthetic function is located in special dorsal projections (44). Typically, gametophytic meristems tend to be terminal or confined to a central position, but in two lycopsid genera the meristem forms a subterminal ring (39) as shown in *Lycopodium* and *Diphasiastrum* of the Lycopodioideae. The actual form of the gametophytes in these two genera, however, is otherwise very different. The buttonlike prothallus of the former is more like that of the outside groups than the peculiar carrot-shaped or rapiform type (42) present only in *Diphasiastrum*. Unbranched gametophytes are the widespread type in practically all pteridophytes (except the obviously specialized ones of certain schizaeas, filmy-ferns, and vittarioids). The tree inhabiting prothallia of the epiphytic *Phlegmariurus* species, where they are known, are branched (43). In this connection, the outgrowths or lobes of Lycopodielloideae, commented on above in connection with photosynthesis, are advanced (44), as they are not found elsewhere except in the (probably very remotely related) Equisetopsida. All other related groups apparently lack such outgrowths. The presence of specialized haploid trichomes or paraphyses among gametangia seems to be unique to the Huperzioideae (45).

The basic condition among Lycopodiaceae otherwise seems to be with the gametangial surfaces glabrous. The nonphotosynthetic gametophytes in the living state tend to be various shades of white, gray, and gray-brown. However, the carrotlike gametophytes of *Diphasiastrum* are usually pigmented orange or orange-brown (46).

Young sporophytes of most lycopsids and other pteridophytes tend to be erect, but in the Lycopodielloideae they are horizontal and creeping (47). In this subfamily, too, the first leaves are actually "protophylls" (48) rather than small versions of microphylls. In two of the genera of Lycopodielloideae, *Lycopodiella* and *Palhinhaea* (but not *Pseudolycopodiella*), there is a specialized structure, the protocorm (50), not found in any of the immediately related living or fossil outside groups (the tuber of *Phyllogossum* evidently not homologous (Bierhorst, 1971)). The foot of the young sporophyte is normally large in genera of Lycopodiaceae but is small (49) in the Lycopodielloideae.

ESTIMATED GROUNDPLAN OF THE ANCESTOR OF MODERN LYCOPODIACEAE

The specialized or advanced states of 50 characters are given above, as best they can be estimated, and each is given a number in parentheses. The primitive or plesiomorphous states may be used to conceptualize the hypothetical ancestral stock from which our present-day genera arose, and this is briefly summarized as follows: Habitat terrestrial; aerial stem branching simply dichotomous, upright; basal stem a horizontal rhizome; roots emerging next to their origin in stem stele, branching dichotomously, the type of root base stele unknown; aerial shoots evergreen, lacking hairs or other emergences; stem actinostelic; gemmae of any kind lacking; shoot branching dichotomous; leaves in 6–12 ranks, monomorphic. Lacking mucilage ducts of any kind. Except for presence of sporangia, sporophylls undifferentiated from trophophylls; sporangia basally attached; strobilus, if present, erect, and if pedunculate, invested by little-differentiated leaves; sporangia reniform, the valves equal, thick-walled, not enclosed in special cavities; sporangial cell walls sinuate and without invaginations, thickened evenly; spores with convex to straight sides and round-pointed angles, the type of sculpture and presence or absence of sculpture on proximal face or whether triradiate ridge reached margin unknown; hybridization between species within a genus common and chromosome pairing in hybrids normal; gametophyte holomyco-parasitic,

subterranean, the meristem central and terminal, the thallus \pm dorsiventral, branching lacking; photosynthetic lobes absent; gametangial paraphyses absent; color whitish to gray-brown; young sporophyte erect, with small microphylls, foot large and protocorm absent.

TREE OF COMPARATIVE DATA

The tree shown in Figure 1 was constructed by assembling the data into what appeared to be the most parsimonious arrangement, using the manual groundplan-divergence principles of Wagner (1962, 1969, 1980), based on the operational idea that phylogeny (i.e., genetic history) is the amount, direction, and sequence of divergence from ancestral groundplans. For the initial layout, only those characters described above were used, and they are numbered on the tree to correspond with the numbers used there. These characters are believed, on the basis of outside evidence, to be uniquely derived or mostly so. Those distinctive character states that could not be assessed as to directionality were added to the tree, and are indicated by letters and numbers, as given in Table 2. The distances between the nodes of the tree are estimated on the basis of all characters, most of them polarized except for the few added later to indicate merely taxonomic differences. Thus, the tree can be used to present visually the broad picture of (systematic) relationships of all the North American Lycopodiaceae. New information can be added to the tree to embody tropical and subtropical genera, and new characters, and the polarities given here can be revised if necessary. If the number of data and taxa becomes very large, it will be necessary to resort to computer algorithms of the manual Wagner Tree.

DISCUSSION OF RESULTS

If the above arguments are valid, then we still must evaluate the traditional generic taxonomy of North American Lycopodiaceae. The application of categories is still arbitrary (Wagner, 1969). Progressively more segregated systems are shown in Table 3, starting with the classical single genus, *Lycopodium*. In order to maintain comparability and consistency of pteridophyte classification, we have kept in mind, for comparison, well-known pairs of sister genera in homosporous pteridophytes. Weak or dubious genera (cf. Table 2A) that are based upon one to few characters should probably be merged (cf. Kramer & Green, 1990): e.g., *Equisetum* and *Hippochaete* (stomates, chro-

TABLE 2. Some possible classifications for North American Lycopodiaceae. (For convenience, the same names are used for the same units, regardless of nomenclatural correctness.)

A.	Genus <i>Lycopodium</i>	E.	Genus <i>Huperzia</i>
B.	Genus <i>Huperzia</i>		Genus <i>Phlegmariurus</i>
	Genus <i>Lycopodium</i>		Genus <i>Lycopodium</i>
C.	Genus <i>Huperzia</i>		Genus <i>Diphasiastrum</i>
	Genus <i>Lycopodium</i>		Genus <i>Palhinhaea</i>
	Genus <i>Lycopodiella</i>		Genus <i>Pseudolycopodiella</i>
D.	Genus <i>Huperzia</i>		Genus <i>Lycopodiella</i>
	Subgenus <i>Huperzia</i>	F.	Subfamily Huperzioideae
	Subgenus <i>Phlegmariurus</i>		Genus <i>Huperzia</i>
	Genus <i>Lycopodium</i>		Genus <i>Phlegmariurus</i>
	Subgenus <i>Lycopodium</i>		Subfamily Lycopodioideae
	Subgenus <i>Diphasiastrum</i>		Genus <i>Lycopodium</i>
	Genus <i>Lycopodiella</i>		Genus <i>Diphasiastrum</i>
	Subgenus <i>Palhinhaea</i>		Subfamily Lycopodielloideae
	Subgenus <i>Pseudolycopodiella</i>		Genus <i>Palhinhaea</i>
	Subgenus <i>Lycopodiella</i>		Genus <i>Pseudolycopodiella</i>
			Genus <i>Lycopodiella</i>

mosome size), *Polypodium* and *Pleopeltis* (scales), *Pteris* and *Schizostege* (splitting of coenosori), *Jamesonia* and *Eriosorus* (no consistent states), *Polystichum* and *Cyrtomium* (reticulate veins), and *Asplenium* and *Camptosorus* (veins and sori). Some other, but still widely accepted, genera (Table 2B, C) are separated by only a moderate number of characters—in fact, considerably fewer than those used here in Lycopodiaceae: *Marattia* and *Angiopteris* (especially type of synangium); *Osmunda* and *Todea* (mainly sporangial arrangement); *Polypodium* and *Pyrrosia* (mainly soral arrangement); and *Dryopteris* and *Ctenitis* (especially trichomes). Few pteridologists would question their validity as genera, in spite of the relatively few characters that separate them, but most would be hesitant about dividing them into subfamilies, although they might set up subgenera (Table 2D) or separate genera (Table 2E). Further splitting is required of single or groups of genera that are so distinct from other singles or groups that they merit placement in distinct subfamilies (Table 2F). Examples from other homosporous pteridophytes are Ophioglossaceae: *Botrychium* and *Helminthostachys* (Botrychioideae) and *Ophioglossum* and *Cheiroglossa* (Ophioglossoideae); Gleicheniaceae: *Gleichenia* and *Dicranopteris* (Gleichenioideae) and *Stromatopteris* (Stromatopteridoideae); Cyatheaceae: *Dicksonia* and *Cibotium* (Dicksonioideae) and *Cyathea* and *Alsophila* (Cyatheoideae); and Dryopteridaceae: *Dryopteris*, *Davallia*, and *Tectaria* (Dryopteridoideae), and *Athyrium* and *Diplazium* (Woodsioideae). We conclude on the basis of these comparisons that the taxonomic division of modern

North American Lycopodiaceae should correspond to Table 2F, i.e., seven genera placed in three subfamilies. The distinguishing characters are numerous, they are accompanied by large gaps and no transitions, they are monophyletic, they involve a number of uniquely derived characters, they do not hybridize with each other, and the segregation level is consistent with other homosporous pteridophytes. The genera fit readily into three subfamilies defined on the basis of their separate patterns of characters and trends.

The two current leaders in the systematics of Lycopodiaceae are Josef Holub and Benjamin Øllgaard, both of whom have made extensive contributions to our understanding of these plants. Their publications (see selected papers in Lit. Cited) contain an enormous amount of information, and they summarize our current knowledge. The classification accepted here for North America conforms, in general, to their concepts except for the assignment of certain ranks. Of the two systems, the ranks of Holub (1983), with all of the genera recognized, are closer to ours; Øllgaard's (1987) treatment has three genera (*Huperzia*, *Lycopodium*, and *Lycopodiella*) in Lycopodiaceae, but includes a number of subgeneric units. Our North American *Phlegmariurus* is in Øllgaard's *Huperzia squarrosa* group; our *Huperzia* is his *Huperzia selago* group; *Lycopodium* includes his *Lycopodium* sect. *Lycopodium*, *Lycopodium* sect. *Annotina*, and *Lycopodium* sect. *Obscura*; *Diphasiastrum*, *Lycopodium* sect. *Complanata*; *Pseudolycopodiella*, *Lycopodiella* sect. *Caroliniana*; *Lycopodiella*, *Lycopodiella* sect. *Lycopodiella*; and *Palhin-*

haea, *Lycopodiella* sect. *Campylostachys*. Holub's most recent treatment (Holub, 1991) of the firmosses recognizes two subgenera under *Huperzia* rather than two genera; his subgenus *Huperzia* equals our genus *Huperzia*, and his subgenus *Subselago* our *Phlegmariurus*. Both Holub and Øllgaard describe a number of tropical and Southern Hemisphere elements, at least some of which can be raised to generic or subgeneric status. However, we believe these non-North American elements will not modify the geographically circumscribed taxonomic treatment given here. This interpretation is summarized in the key that follows:

TECHNICAL KEY TO NORTH AMERICAN
SUBFAMILIES AND GENERA

- 1a. Sporophylls like trophophylls, photosynthetic; plants epiphytic, epipetric, or terrestrial; roots running from the apex through cortex before emerging; leaves lacking mucilage canals; rhizome absent; paraphyses present among gametangia; spores foveolate-fossulate; chromosomes $x = 67-68$ *Huperzioideae*
- 2a. Plants epiphytic, mostly pendent at maturity; lacking gemmiphores and gemmae; gametophytes branched; spore angles pointed, spore sides straight or convex; proximal face unpitted, hanging firmosses *Phlegmariurus* Holub
(1 orthospecies, 0 nothospecies in North America)
- 2b. Plants terrestrial or epipetric, mostly erect at maturity; producing specialized lateral gemmiphores among the leaves bearing flattened green gemmae; gametophytes unbranched; spore angles truncate, spore sides concave; proximal face pitted, gemma firmosses *Huperzia* Bernh.
(6 orthospecies, 7 nothospecies)
- 1b. Sporophylls \pm strongly modified, unlike trophophylls, nonphotosynthetic at maturity; plants terrestrial or semiaquatic; leaves with basal mucilage canals; roots emerging immediately, scattered along rhizome; rhizome present; paraphyses absent among gametangia; spores various but not foveolate-fossulate; chromosome x numbers various.
- 3a. Spore sculpture reticulate; capsule wall cells sinuate to invaginate; root stele like rhizome stele at base; gametophyte subterranean, nonphotosynthetic, growing by a ring meristem; archegonia long, persistent *Lycopodioideae*
- 4a. Shoots round-branched, the mature leaves monomorphic and separate, in 6-8 ranks; sporangial wall cells with invaginations and evaginations; gametophytes gray or brown, flat, buttonlike and convoluted when mature; chromosomes $x = 34$, common clubmosses *Lycopodium* L.
(6 orthospecies, 0 nothospecies)
- 4b. Shoots flat-branched (with 1 exception), the leaves mostly dimorphic or

trimorphic and overlapping and (or) imbricate, in 4-5 ranks (in *D. sitchensense* leaves 5-ranked and morphologically as in juveniles); sporangial wall cells smoothly sinuate; gametophytes orange pigmented, narrowly top-shaped, nonconvoluted; chromosomes $x = 23$, flat-branched clubmosses

- *Diphasiastrum* Holub
(5 orthospecies, 6 nothospecies)
- 3b. Spore sculpture rugulose; capsule walls straight; root stele various; gametophytes subsurficial, with photosynthetic lobes; archegonia short, ephemeral ... *Lycopodielloideae*
- 5a. Plants terrestrial; upright shoot complexly dendroidly branched; basal root stele like stem; spore laesura groove not reaching the margin; spore proximal faces not sculptured; chromosomes $x =$ ca. 55, tropical treelike clubmosses ... *Palhinhaea* Franco & Carv.
(1 orthospecies, 0 nothospecies)
- 5b. Plants semiaquatic; upright shoot simple; basal root stele C-shaped in section; spore laesura groove reaching spore margin; spore proximal faces sculptured; chromosomes not $x =$ ca. 55.
- 6a. Peduncle leafy; sporophylls resembling trophophylls; horizontal shoot rounded, with uniform leaves \pm spreading to erect; vein al mucilage canals present; $x = 78$, common bog clubmosses *Lycopodiella* Holub
(6 orthospecies, 8 nothospecies)
- 6b. Peduncle mostly bare with scattered scalelike appendages; sporophylls much reduced, horizontal shoot flat, the leaves unequal, the larger ones in two rows and nearly flat on the substratum; vein al mucilage canals absent; $x = 35$, Carolina bog clubmosses *Pseudolycopodiella* Holub
(1 orthospecies, 0 nothospecies)

LITERATURE CITED

BIERHORST, D. W. 1971. *Morphology of Vascular Plants*. Macmillan, New York.

BRUCE, J. G. 1972. Observations on the occurrence of prothallia of *Lycopodium inundatum*. *Amer. Fern J.* 62: 82-87.

———. 1975. Systematics and morphology of subgenus *Lepidotis* of the genus *Lycopodium* (Lycopodiaceae). Ph.D. Dissertation. University of Michigan, Ann Arbor.

———. 1976a. Comparative studies in the biology of *Lycopodium carolinianum*. *Amer. Fern J.* 63: 919-924.

———. 1976b. Gametophytes and subgeneric concepts in *Lycopodium*. *Amer. J. Bot.* 62: 919-924.

———. 1979. Gametophyte of *Lycopodium digitatum*. *Amer. J. Bot.* 66: 1138-1150.

——— & J. M. BEITEL. 1979. A community of *Ly-*

- copodium* gametophytes in Michigan. Amer. Fern J. 69: 33-41.
- FERNALD, M. L. 1950. Gray's Manual of Botany, 8th ed. American Book, New York.
- FREEBERG, J. A. & R. H. WETMORE. 1957. Gametophytes of *Lycopodium* as grown *in vitro*. Phytomorphology 7: 204-217.
- HOLUB, J. 1975. *Diphasiastrum*, a new genus in Lycopodiaceae. Preslia 47: 97-100.
- . 1983. Validation of generic names in Lycopodiaceae; with a description of a new genus *Pseudolycopodiella*. Folia Geobot. Phytotax. 18: 439-442.
- . 1985. Transfers of *Lycopodium* species to *Huperzia*: with a note on generic classification in Huperziaceae. Folia Geobot. Phytotax. 20: 67-80.
- . 1991. Taxonomic changes within Lycopodiales. Folia Geobot. Phytotax. 26: 81-94.
- KRAMER, K. U. & P. S. GREEN (editors). 1990. Vol. I. Pteridophytes and gymnosperms. In: K. Kubitzki (editor), The Families and Genera of Vascular Plants. Springer-Verlag, Berlin, Heidelberg.
- ØLLGAARD, B. 1975. Studies in Lycopodiaceae, I. Observations on the structure of the sporangium wall. Amer. Fern J. 65: 19-17.
- . 1979. Studies in Lycopodiaceae, II. The branching patterns and infrageneric groups of *Lycopodium* sensu lato. Amer. Fern J. 29: 49-61.
- . 1987. A revised classification of the Lycopodiaceae s. l. Opera Bot. 92: 153-178.
- PICHI SERMOLLI, R. E. G. 1977. Tentamen pteridophytorum genera in taxonomicum ordinem redigendi. Webbia 31: 313-512.
- STEVENSON, D. W. 1976. Observations on phyllotaxis, stelar morphology, the shoot apex and gemmae of *Lycopodium lucidulum* Michaux (Lycopodiaceae). Bot. J. Linn. Soc. 72: 81-100.
- STEWART, W. N. 1983. Paleobotany and the Evolution of Plants. Cambridge Univ. Press, Cambridge.
- TAYLOR, T. M. 1981. Paleobotany. McGraw-Hill, New York.
- THOMAS, B. A. & R. A. SPICER. 1987. The Evolution and Paleobotany of Land Plants. Chatham, Kent, Great Britain.
- TRYON, A. F. & B. LUGARDON. 1990. Spores of the Pteridophyta. Springer-Verlag, New York.
- WAGNER, F. S. 1992. Cytological problems in *Lycopodium* sens. lat. Ann. Missouri Bot. Gard. 79: 718-729.
- WAGNER, W. H., JR. 1962. The synthesis and expression of phylogenetic data. Pp. 273-277, 415-418 in L. Benson (editor), Plant Taxonomy. Roland Press, New York.
- . 1969. The construction of a classification. Pp. 67-90 in C. Sibley (editor), Systematic Biology. U.S. Natl. Acad. Sci. Publ. 1962, Washington, D.C.
- . 1980. Origin and philosophy of the ground-plan-divergence method of cladistics. Syst. Bot. 5: 173-193.
- WHITTIER, D. P. 1981. Gametophytes of *Lycopodium digitatum* (formerly *L. complanatum* var. *flabelliforme*) as grown in axenic culture. Bot. Gaz. (Crawfordsville) 142: 519-524.
- WILCE, J. H. 1965. Section *Complanata* of the genus *Lycopodium*. Beih. Nova Hedwigia 19. J. Cramer, Weinheim.
- . 1972. *Lycopodium* spores. I. General spore patterns and the generic segregates of *Lycopodium*. Amer. Fern J. 62: 65-89.

NEOTROPICAL LYCOPODIACEAE—AN OVERVIEW¹

Benjamin Øllgaard²

ABSTRACT

Approximately 185 species of Lycopodiaceae are known to occur in the Neotropics: ca. 150 belong in the genus *Huperzia*, ca. 8 in *Lycopodium*, and ca. 25 in *Lycopodiella*. The species are enumerated according to assumed relationship, with information of the most important synonyms, a summary of their distribution, comments on their morphology and variability, and reference to selected illustrations. Species delimitation is problematic throughout the family. This is due to the simple morphology and the plasticity of the characters. Morphogenesis seems unstable in many species and may be strongly affected by environmental factors. Most characters are variable within a species, e.g., stem thickness, number of leaf orthostichies, leaf crowding, leaf direction, development of teeth on leaf margins, color, degree of heterophyllous differentiation. Often the diagnostic features of closely related species are without apparent adaptive significance. Hybridization is believed to occur rather freely, but the putative hybrids often have normally developed spores. Three new combinations, *Huperzia tubulosa* (Maxon) B. Øllg., *Huperzia watsoniana* (Maxon) B. Øllg., and *Lycopodiella torta* (L. Underw. & F. Lloyd) B. Øllg., are proposed.

The present paper attempts to survey the diversity and variation of the species of Lycopodiaceae sens. lat. in the area covered by *Flora Neotropica*, an area roughly defined as the parts of the Americas between the Tropics of Cancer and Capricorn. It presents preliminary results of studies prior to a monograph of the family for *Flora Neotropica*.

No earlier studies apply to the species in this area in its entirety, with the exception of an unsatisfactory worldwide synopsis by Nessel (1939). However, several recent regional treatments are available, e.g., for parts of Mexico (Mickel & Beitel, 1988; Smith, 1981); Guatemala (Øllgaard, 1983); Costa Rica to Colombian Chocó (Lellinger, 1989); Lesser Antilles, Jamaica, Puerto Rico, and the Virgin Islands (Proctor, 1977, 1985, 1989); Venezuela (Øllgaard, 1985b); Surinam (Kramer, 1978); Ecuador (Øllgaard, 1988); and Brazil (Øllgaard & Windisch, 1987). A paper by Rolleri (1980) treated *Lycopodium* [*Huperzia*] section *Crassistachys* Herter, a group of mainly neotropical distribution.

The total number of species contained in the family is uncertain, but is estimated to exceed 350. Approximately 185 species are known in the Neo-

tropics, but several remain to be described, especially from the Andes, and several are expected to be discovered as a result of future exploration in the area. Detailed study of some of the complex and yet poorly understood species may add to the number of recognized species.

The special problems encountered in the family relate mainly to interpretation of morphological characters. The nomenclatural problems are relatively few and generally not very complex. This may be because relatively few botanists have been involved in the study of the family, and horticultural interest in the family has been sparse. The plants are generally small and easily collected, so the type material generally is of good quality. The most serious nomenclatural problems relate to the numerous taxa described in the years 1927–1940 by Hermann Nessel. Fortunately, Nessel's herbarium is preserved in Bonn, but numerous problems of typification of his names remain to be solved, due to poor or inane diagnoses, inconsistency of specimen citations with illustrations, and inaccurate, erroneous, or perhaps falsified label information.

The taxonomic characters and interpretations of their variation are discussed in the following, in

¹ Parts of this paper were presented at the Lycopod symposium of the AIBS Annual Meeting in Toronto, 1989. I am grateful to the organizers, Judith E. Skog and William DiMichele, and to David B. Lellinger, for arranging funds and facilities for the participation and related research in the Smithsonian Institution and the New York Botanical Garden. I thank Joseph M. Beitel, R. James Hickey, John T. Mickel, and W. H. Wagner, Jr. for stimulating discussions of the subject during the symposium, and David Lellinger and W. H. Wagner, Jr. for many useful suggestions on the manuscript. Economic support received from the U.S. National Science Foundation and the Suzanne Liebers Erickson Danish Exchange Fund of the Smithsonian Institution is gratefully acknowledged. Drawings by Kirsten Tind.

² Herbario QCA, P. Universidad Católica del Ecuador; present address: Institute of Biological Sciences, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark.

the context of the genera and species groups where they are most relevant. The following features contribute to the problems of species delimitation in general: simple morphology, plasticity of characters in response to environmental factors, apparent lack of adaptive significance of several characters used for identification or recognition, and an apparently somewhat labile intrinsic control of morphogenetic processes. This means that species often are vaguely defined, based on common sense and experience rather than definite sets of characters. The ecology of species, e.g., the altitudinal range may yield important characters useful for identification.

ENUMERATION OF THE SPECIES

The following enumeration of the neotropical species follows the classification of Øllgaard (1987, 1989a). According to that classification three genera occur in the Neotropics, *Huperzia*, *Lycopodium*, and *Lycopodiella*. However, it should be noted that within each of the three genera as construed here there are groups, here treated as sections, which may well be treated as separate genera because the extent and number of differences between these groups exceeds that of widely accepted fern and seed-plant genera. Wagner & Beitel (1992) discuss this problem and call attention to the importance of comparability in generic definition.

Within each genus, as here construed and within the informal and formal groups, the species are arranged in so far as possible in a linear sequence according to assumed relationship.

After each accepted species name synonyms are given in parentheses. The descriptions of genera and sections include only the neotropical members of the groups. A summary of the distribution and ecology, and references to selected published illustrations conclude the entry when appropriate. For additional information on original publications, nomenclature, and types of the species, the reader is referred to the index by Øllgaard (1989a).

HUPERZIA BERNHARDI

Sporophytes terrestrial or epiphytic, isotomously branched throughout except in connection with bulbil formation (*H. selago* group), the branch portions between dichotomies being referred to as divisions. Growth habit pendent to recurved, erect, or ascending. Stele occupying a small proportion of the stem diameter, with radially arranged xylem groups. Branches are all similar, or in some terrestrial species differentiated (heteroblastic) into

prostrate, sometimes subterranean (vs. erect) aerial branches. Roots penetrate the stem cortex longitudinally before emerging as one basal tuft. In some species with heteroblastic shoots, the roots may emerge more directly, at soil contact. Trophophylls and sporophylls conform, gradually dimorphic or in some species sharply dimorphic. Sporophylls lacking mucilage cavities, not ephemeral, remaining chlorophyllous and functioning like trophophylls long after the sporangium dehiscence, not specialized like the sporophylls in the other genera. Sporangia in species with constricted distal branches borne predominantly in these, but constricted branches not readily comparable with the strobili of the other genera, as often seen in the literature, both because of the unspecialized sporophylls and their being intermixed, often randomly, with conform trophophylls. Sporangia axillary, with a short slender stalk, isovalvate, with thickened, lignified, sinuate side walls in epidermal cells. Spores foveolate-fossulate. Gametophytes unknown in the area, but subterranean, mycoparasitic, elongate, cylindrical or with bilateral symmetry, with pluricellular, uniseriate hairs among the gametangia in related, extralimital species.

Virtually cosmopolitan, with perhaps 300 species, by far the largest of the three genera, with approximately 150 species in the Neotropics.

The species are diverse with respect to growth habit, size, leaf differentiation, and a variety of adaptations to protected or exposed growth conditions. Several striking types of growth habit and leaf differentiation are apparent in the genus. However, nearly all of these types are interconnected by intermediates, so that the species appear to form a virtually continuous morphological series. They were divided into 22 informal and vaguely defined groups by Øllgaard (1987). Twelve of these groups are represented in the Neotropics. The comments on relatives of the species of the groups often indicate that there are several points of uncertain group delimitation. Also, the occasional formation of hybrids between both ecologically and morphologically widely different species, e.g., *H. reflexa* × *H. linifolia* (Øllgaard, 1985a), indicates that some of these groups may be more closely related than their morphological characters suggest. Only one group of specialized species, including the type of the genus, *Huperzia selago* (L.) Mart. & Schrank, is so distinct that it may merit formal recognition.

These informal groups and their features of variation and distribution are presented below. The most important characters used for classification